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Dichogamy in flowering plants[1]

A. B. Stout

(WITH FIVE TEXT FIGURES)

The term 'Dichogamie' was first used by Sprengel in 1793 to designate the condition of an hermaphrodite flower when its two kinds of sex organs mature in different intervals of time. This condition had previously been described by Kölreuter (1761) but it remained for Sprengel to apply the name *dichogamy* and to recognize both the male-female sequence ('dichogamia androgyna') and the female-male sequence ('dichogamia gynandra'). These two conditions were later named *protandry* and *protogyny* by Hildebrand (1867), and proterandry and proterogyny by Delpino (1868–1875). In discussing the terms used for these conditions, Bennett (1870) remarks that the term 'non-dichogamy' does not seem so happy, and proposes instead the word *synacmy*, and to continue the same derivation he proposes the use of heteracmy instead of dichogamy. The term dichogamy has, however, remained in very general use, and besides it seems desirable to use the prefix 'hetero' with the word dichogamy (*heterodichogamy*) to refer to the condition when both protandry and protogyny or when various degrees of dichogamy exist among the flowers of one plant or among the individuals of a species. In this paper the terms given above in italics will be given preference.

A few writers, Delpino especially, have sometimes spoken of dichogamy as a general law of cross-pollination embracing many or all adaptations, morphological as well as physiological, for cross-fertilization. But in its generally accepted use the term dichogamy retains the fundamental meaning as conceived by Sprengel in that it refers solely to differences in the periods of time during which the two sexes, represented by stamens and pistils, are mature.

[1] Presented at the joint session of section G of the American Association for the Advancement of Science, the Botanical Society of America, the American Phytopathological Society, and the American Society of Plant Physiologists at Nashville, Tenn., 28 December 1927.

[The Bulletin for February (55: 91–140) was issued 15 March 1928]

Since Sprengel's time it has been established that dichogamy, as he knew it, is operating in the hermaphrodite flowers of many species. But certain further developments of dichogamy have been discovered and of these the most important are: *first*, that dichogamy also exists in monoecious plants, in plants and species that are polygamous, and in dioecious species; *second*, that heterodichogamy, as defined above, may exist; and, *third*, that the condition of dichogamy may extend to an entire plant as a unit, to a group of plants, and to an entire species as such.

Evidently there are few hermaphrodite flowers in which the period of the maturity of stamens and the period when the pistil or the group of pistils is mature are exactly coincident in the single flower. Thus, in a flower of certain species of *Lilium*, the anthers begin to dehisce before the pistil is receptive, but unless insects promptly remove the pollen the shedding of pollen continues during the time that the pistil is receptive. There is then synacmy (non-dichogamy)—a condition probably primitive in hermaphrodite flowers and evidently still quite general in them.

The first step in dichogamy is seen when the two periods of staminate and pistillate maturity for an individual flower overlap only in part. This is known as incomplete dichogamy in a flower. Probably the flowers of most species having hermaphrodite flowers are either synacmous or incompletely dichogamous. But a still further development gives dichogamy that is complete, and the individual flower is, functionally, either first male and then female (protandrous) or is first female and then male (protogynous) according to the sequence of the maturity.

The condition of complete protandry, as it is usually seen in hermaphrodite flowers, may be illustrated in the Japanese bell-flower (*Platycodon grandiflorum*). The few stamens dehisce fully soon after the flower opens. Only after the anthers are shrivelled and the pollen is removed or is no longer viable do the stigmatic lobes of the pistil unfold and their inner surfaces become receptive. Dichogamy is thus complete in a flower and it operates in quite the same degree in all flowers on the plant throughout the season of blooming.

The flower behavior of such a plant may be represented somewhat schematically for a flowering period of ten days in the section showing protandry in figure 1.

On the first day of blooming, one or more flowers open and perhaps shed pollen until some time the following day, here represented by dots. The pistils of these same flowers are receptive, let us say, in the third and fourth days—here represented by a continuous line on the same level with the first

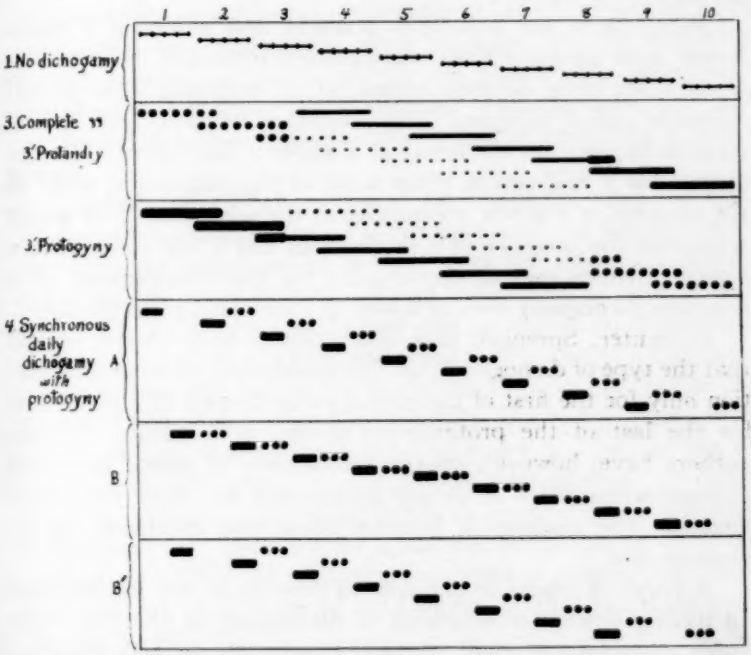

FIG. 1. Schematic representation of types of flower behavior in plants having hermaphrodite flowers for an arbitrary period of ten days of blooming. The chart is for the hours of daylight only.

The dots represent pollen-shedding, and a continuous line represents a period when pistils are receptive. The collective behavior of a set of flowers beginning anthesis on the same day is represented at one level. The periods when the entire plant can function as one sex only are shown by the larger dots and by the heavier lines. Discussion of each of the types here represented is given in the text.

series of dots. On each day of the blooming period, except the last two, a set of flowers starts in the cycle of anthesis. Dichogamy is complete for each flower and for the group of flowers of each set. For the plant as a whole there are three sections to its season of bloom. There is a mid-season period when

close-pollinations are possible, and there are two end-season periods in each of which the plant functions as one sex only. In case there is the same degree of protogyny in hermaphrodite flowers, the relations for a plant as a whole are the reverse of those in protandry and are as represented in the section showing protogymy of figure 1.

When there are numerous stamens and pistils in a single flower, as in species of Ranunculaceae and Rosaceae, the members of each sex often develop somewhat in succession over a considerable period of time. This condition tends to give incomplete dichogamy for the flower as a whole in that there is greater chance for a mid-period when some of the pistils and some of the stamens in a flower are mature at the same time. It would seem that the presence of a single pistil and a few stamens in a flower provides greater opportunity for the development of a complete dichogamy such as is seen in *Platycodon grandiflorum*.

Kölreuter, Sprengel, and many others have clearly stated that the type of dichogamy just discussed compels cross-fertilization only for the first of the protogynous flowers of a plant and for the last of the protandrous flowers of a plant. Certain authors have, however, spoken erroneously of *plants* as dichogamous when there is simply dichogamy for their *individual flowers*. The distinction between these two conditions is an obvious one.

A group of plants of one species growing in one locality and all having flowers of one kind of dichogamy of the type now under consideration will provide conditions as follows:—the flowers of the first and the last days of the period of collective blooming can function only in hybridization. Throughout the greater portion of the blooming period cross-pollinations within the species are possible just as close-pollinations within the individual plant are possible during its mid-period of bloom.

For many years it was considered that the different individuals of a species are all alike in respect to the kind of dichogamy which they possess. Evidently it was not until 1870 (Batalin, 1870) that it was found that in certain species some individuals may have protandrous flowers and others have protogynous flowers. It is now known that these extreme differences in the kind of dichogamy may, in certain cases, also be seen among the flowers of one plant. Thus in the skunk cabbage (*Spathyema*

foetida) some plants have all flowers protandrous, others have all flowers protogynous, and others have some flowers protandrous and some protogynous (Atkinson, 1898, pages 356–360). There is thus heterodichogamy in certain individuals and also heterodichogamy among the plants of this species.

In none of the developments thus far mentioned is dichogamy complete for the entire plant throughout the entire season of its blooming. But dichogamy does advance to this degree in certain monoecious plants, and among plants with hermaphrodite flowers it is known in avocados. This condition was first discovered in monoecious plants, in which its operation is rather simple.

The butternut (*Juglans cinera*) illustrates the condition typical for monoecious plants. On certain plants the female flowers are receptive before pollen is shed from the staminate flowers below on the same branch. These differences in time of maturity may be closely coördinated and synchronized throughout the many branches of a tree, and when this is complete the entire tree functions as a female for something like the first half of the season of flowering and as a male for the last half as represented in the section showing protogyny in figure 3. But in not all trees of the butternut are the flowers protogynous. In some trees the staminate flowers are first to mature. There is a heterodichogamy that provides for a double reciprocation in cross-pollination. That this situation may exist in monoecious plants was evidently first reported by Delpino in 1875 for the species *Juglans regia*.

Some of the most exact studies of the flower behavior in monoecious plants have been made with certain cultivated clons of pecans and filberts. In the pecans Stuckey (1916) finds two main groups of individuals and clons. In one there is synacmy, or at least only a slight protandry. In the other group there is protogyny with the pistils maturing from two to ten days before pollen is shed. In the filberts, Schuster (1924, 1927) finds that of the ten clonal varieties studied by him, three are not dichogamous though the periods of maturity do not coincide, five are incompletely dichogamous, and in two the protandry is practically complete. The chart showing the flower-behavior for ten varieties of filberts arranged from Schuster's data is here given in figure 2.

Thus in both filberts and pecans, in some individuals the staminate and the pistillate flowers mature together or there is a decided overlap in their periods of maturity. Possibly the same situation exists in the butternuts and walnuts. At least this seems to be the case for certain clons of English walnuts grown commercially in solid-block plantings.

A still further type of dichogamy for monoecious plants exists in chestnuts. The lower catkins on the branches bear

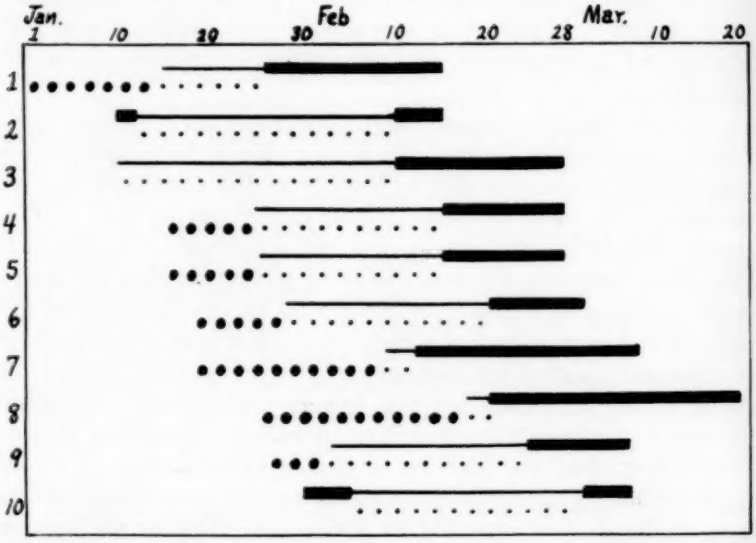

FIG. 2. The blooming dates of filberts. Four year average at Corvallis, Oregon. Dots indicate periods of shedding pollen and continuous lines indicate periods when pistils are mature. From top to bottom varieties as follows: (1) Fertile de Coutard, (2) Montebello, (3) Barcelona, (4) White Aveline, (5) Red Aveline, (6) Daviana, (7) Nottingham, (8) Cosford, (9) Du Chilly, and (10) Merveille de Bolwyller.

only staminate flowers and these mature and shed pollen first in the season of bloom, while the catkins which bear pistillate flowers are still immature. The pistillate flowers are next to mature. Still later there is maturity of those staminate flowers that are situated on the distal portions of the same catkins which bear pistillate flowers.

Exact studies of the dates of anthesis for chestnuts have apparently never been made, but a chart showing the behavior

as reported for certain plants is somewhat as represented in section 8 of figure 3. There are two end-season periods of pollen-shedding from two different kinds of catkins with a mid-period for the maturity of pistils. This we may call duodichogamy. What the variations are in this type of dichogamy and what reciprocations may be operating are at present undetermined. In the chart the periods are shown with over-

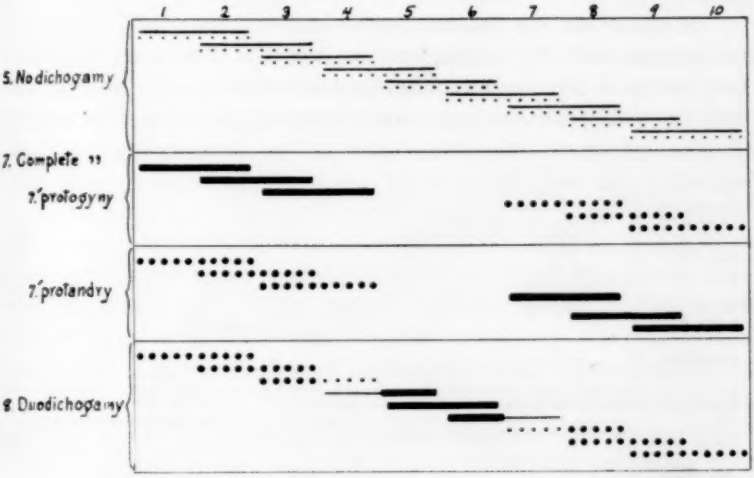

FIG. 3. Schematic representation of the types of flower behavior that are to be found in monoecious plants. When there is no dichogamy staminate flowers and pistillate flowers are mature or functional each day during the period of bloom. When the dichogamy is complete staminate and pistillate flowers function at different dates of the flowering period, giving either protogyny or protandry, and the entire plant functions as one sex only for something like half of the season of bloom. The case of duodichogamy as known in chestnuts is represented in the section bearing the number 8.

lappings but it may be that in some individuals these do not exist.

The chestnuts (Schneck, 1880; Stout, 1926) and the filberts (Schuster, 1924, 1926) are known to be decidedly self-fruitless, both when a single plant grows in isolation or when plants of one clon are grown in a solid block. A complete dichogamy will produce this condition. But synacmous clons of filberts may be equally self-fruitless, hence it is clear that self-incompatibility

in fertilization may operate together with dichogamy in a species to limit self-fruiting.

The data available for filberts, pecans, butternuts, and walnuts suggest that heterodichogamy and incomplete dichogamy may be rather frequent in monoecious species and that the variations which exist may involve synacmy, protogyny, and protandry in all possible combinations and degrees of development.

In dioecious species the individual is unisexual. There is no opportunity for dichogamy within the flower or between two kinds of flowers on a plant. Here dichogamy can operate only between plants or groups of plants in respect to the relative

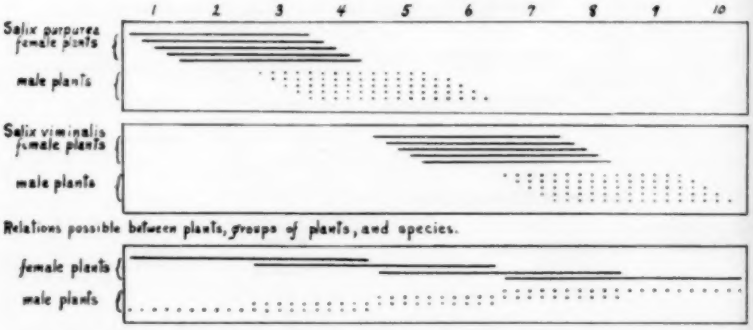

FIG. 4. Schematic representation of dichogamy in dioecious species as described by Kerner, showing conditions which promote hybridization.

seasons of blooming. It is stated by Kerner (1891, vol. 2, p. 311) that in certain species of *Salix* the flowers of female plants are ready for pollination before male plants of the same species growing in the same locality are shedding pollen. The relative behavior of the male and female plants of two such species, as Kerner describes it, may be shown in the charts of figure 4. The restrictions to pollinations within each species and the opportunities for hybridization between them are obvious.

In considering the operation of dichogamy, we note that the presence of unisexual flowers on a plant, as in monoecious plants, and of unisexual individuals in a dioecious species automatically reduces the scope of dichogamy, and simplifies its operation for a plant as a whole. The greatest opportunity for the expression

of dichogamy in all of its aspects is in plants with many hermaphrodite flowers which bloom day after day for a somewhat extended period or season. In such plants the opportunities for dichogamy within the flower, within sets of flowers, and between sets of flowers are all retained along with chances for the extension of dichogamy to a plant as a unit and to a group of individuals. And so, for the most comprehensive expressions of dichogamy now known, we turn to plants with hermaphrodite flowers and consider the flower behavior in avocados.

The flowers of all avocados, except for a few anomalous types, are perfect, rather simple in structure, and very uniform. They are all protogynous with two distinct periods of anthesis. In the first anthesis the flowers function only as females. In the second anthesis the same flowers function as males and present a very different appearance. (For illustrations and more complete descriptions see Stout, 1923, 1927.) All individuals grown from seed and all clonal varieties fall into two groups. In one group which has been designated group *A* the flower behavior is as follows:—In the early forenoon a set of flowers open in unison for the first or female anthesis. About noon these flowers close almost in unison and they remain closed until the afternoon of the next day when they are open for the second or male anthesis. The sequence of following sets proceeds with remarkable regularity under favorable weather and brings two different sets into anthesis each day as represented in *A* of chart *4* in figure 1. In the forenoon one set is in its first or female anthesis; in the afternoon another set, which is an older set, is in its second or male anthesis.

For trees of the *B* group the flowers are also protogynous but the first anthesis is in the afternoon and the second anthesis is in the forenoon either of the following day or of the second day. With the sequence of sets having these cycles of dianthesis, plants function as males in the forenoon and as females in the afternoon (*B1* and *B2* in chart *4* of fig. 1).

Thus in respect to the daily alternation of sexes there is a double reciprocation between the two groups of plants. In the forenoon pollen can be carried from a plant of the *B* group to a plant of the *A* group and in the afternoon the relation is reversed. The varietal, seasonal, and daily variations, and the probable evolution of the various types of dichogamy in avocados

have been discussed elsewhere (Stout, 1923, 1927). It is the general rules of behavior that are presented here.

Charts representing the principal types of dichogamy as they are now known in flowering plants are given in figures 1, 3, and 4. There are other types that are possible and that are suggested by certain observations that have been made. Especially is this the case in respect to specialization in daily alternation and to duodichogamy. The former could readily develop in monoecious plants and also in hermaphrodite flowers that open for a single anthesis. There may also be many extensions of duodichogamy that remain to be discovered.

Modifications in the flower behavior of a plant as a whole are to be seen for plants which possess various proportions of hermaphrodite, pistillate, and staminate flowers. These modifications likewise extend to the relations of intra-group dichogamy when there are various combinations of hermaphrodite and unisexual flowers for the different individuals. There are no data available from which accurate charts can be constructed representing the flower behavior of a group of plants of the red maple (*Acer rubrum*), of the horse-chestnut (*Aesculus Hippocastanum*), or of various species of the Compositae. But in all cases, unless there be some entirely new types of dichogamy, the behavior can be represented by combining different charts and certain parts of the charts of figures 1, 3, and 4 both of vertical and of horizontal sections according to the conditions.

We may combine the flower behavior of the different sets of flowers and reduce the charts showing types of dichogamy to the behavior of a plant as a unit, thus making comparisons somewhat easier (fig. 5).

There are three main aspects in the operation of dichogamy in its effect on pollination:—

First, there are the limitations which it imposes on self-pollinations, on close-pollinations, and on cross-pollinations within the species. The degree to which these are operating in the various types of dichogamy are represented in the group of charts at the left, the scope of enforced cross-pollinations being given in the heavier lines and dots.

Second, there are the various means by which dichogamy provides for cross-pollination within the species. These reciprocations are represented in the charts at the right.

Third, there is the extent to which dichogamy promotes cross-fertilization between species.

For plants with hermaphrodite flowers, complete dichogamy in the flowers restricts or prevents all self-pollinations and all close-pollinations within each set. As it ordinarily operates, it extends also to the plant as a whole for the end-season periods and, considering these alone, dichogamy operates in the entire plant in one alternation represented by the heavy line and dots in the chart for complete dichogamy (*3* in fig. 5).

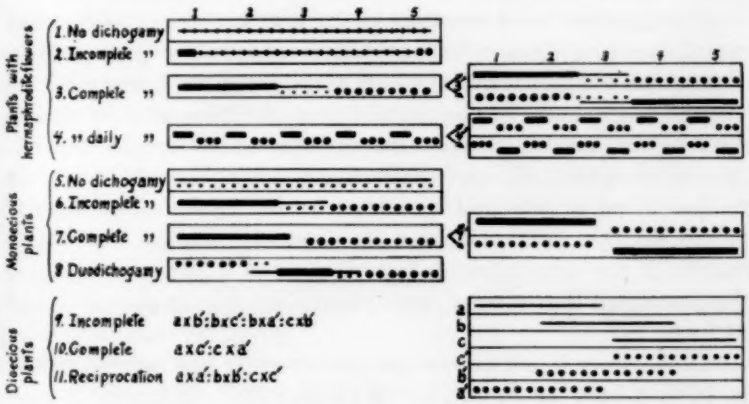

FIG. 5. Schematic representation of the main types of flower behavior reduced for a plant as a unit and for an arbitrary period of five days of daylight. The types of reciprocation are shown at the right. The extent to which cross-fertilization is necessary in such cases is indicated by the larger dots for the pollen-shedding and by the heavier lines for pistil-maturity.

In avocados with their hermaphrodite flowers one alternation of dichogamy is completed each day by a division of the hours of daylight between two different sets of flowers, one in the female anthesis and the other in the male anthesis (*4* in figs. 1 and 5).

In monoecious plants dichogamy operates between the two groups of staminate and pistillate flowers and readily extends end-season periods until they are completely separated (*7* in figs. 3 and 5). There is thus one cycle of alternation for the plant as a unit.

Continuing to dioecious plants, which are structurally of one sex, dichogamy operates only to reduce cross-pollinations within the species (fig. 4, and *9* and *10* in fig. 5).

Thus the operation of one kind of dichogamy in any species reduces the chances for the perpetuation of the species to a greater or less extent. A complete daily dichogamy of one type, as the *A* type in avocados, almost completely eliminates self-fruiting within a group of plants. The same is true of complete protandry or protogyny in a monoecious species. Through such an overspecialization of dichogamy, an entire species becomes subject to disappearance although it may be merged with other species through hybridization. We have no accurate data as to how frequently this is occurring in nature.

On the other hand there are in the climax types of dichogamy certain reciprocations which provide for complete cross-pollination within the species, and which counteract the overspecialization of one type. In the usual types of dichogamy in species with hermaphrodite flowers and in monoecious species there is heterodichogamy (*3′* and *7′* in fig. 5). In the avocados the reciprocation is obtained by reciprocating cycles of protogyny (*4′* in fig. 5). Reciprocation in dioecious plants is solely a matter of the simultaneous flowering, or of a partial overlap in the seasons of flowering of male plants and female plants (*9* and *11* in fig. 5).

Dichogamy is not one simple process. It has many aspects. In kind it may be protandry or protogyny. In degree it may be partial or complete. In scope it may operate more or less independently in a single flower, in a set of flowers opening together, in all flowers of one sex on a plant, in a plant as a whole, in a group of plants, or in all plants of one sex in a species. In extent of time the cycle of dichogamy may be complete in one day, it may extend to end-season portions of a season of bloom, or it may operate in one cycle for the entire period of blooming. In respect to the number of alternations of cycles of dichogamy, in plants having many flowers, there may be many cycles or there may be only one. Dichogamy may also operate within a single sex as is seen in duodichogamy.

That the various aspects of dichogamy have a basis in heredity is obvious. The presence of heterodichogamy and duodichogamy among flowers of a single individual indicates that there is also a regulation in development. The expressions of dichogamy are often delicately regulated in response to such external stumuli as light and temperature with much abnormal

procedure under unfavorable weather conditions. This is well shown in the avocados (Stout, 1923, 1927).

Much remains to be learned regarding dichogamy:—(1) as to the facts regarding its operation, (2) as to its relation to the unfruitfulness in fruit and nut crops, especially in those grown as clonal varieties, (3) as to the mechanism of its physiological expression, (4) as to its heredity and evolution, (5) as to its significance to vegetative and reproductive vigor, and (6) as to its importance in hybridization and the evolution of species.

For the past fifty years, knowledge of dichogamy has made little advance. As a result the phenomena of dichogamy now present a fertile field for investigation.

Dichogamy exists widely in all types of flowering plants. It operates as a potent means of promoting and forcing cross-pollinations within and between species. The rôle which dichogamy plays in evolution through hybridization is, evidently, an important one.

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Notes on Fabaceae—XI

PER AXEL RYDBERG

ATELOPHRAGMA Rydberg

6. STRIGULOSA

Pod glabrous.
- Calyx-lobes deltoid, one-fourth as long as the tube; corolla usually tinged with purple ..... 23. *A. Painteri*
- Calyx-lobes subulate, half as long as the tube or longer.
  - Corolla bluish-purple, strongly striate; bracts ovate or lanceolate ..... 24. *A. toluccanum*
  - Corolla white or tinged with purple; bracts subulate.
    - Body of the pod 3–4 cm. long.
      - Leaflets oblong; stipe of the pod longer than the calyx-tube.
        - Calyx short-hairy, its teeth shorter than the tube ..... 25. *A. jaliscense*
        - Calyx long-hairy, its teeth fully as long as the tube ..... 26. *A. zacatecanum*
      - Leaflets obovate, retuse; stipe of the pod shorter than the calyx-tube ..... 27. *A. tioides*
    - Body of the pod 1–2 cm. long; leaflets elliptic.
      - Stipe of the pod longer than the calyx tube; calyx-teeth nearly as long as the tube; corolla 10 mm. long ..... 28. *A. strigulosum*
      - Stipe shorter than the calyx tube.
        - Calyx not densely black-hairy, the teeth less than half as long as the tube; raceme lax, few-flowered; corolla 7 mm. long ..... 29. *A. hidalgense*
        - Calyx densely black-hairy, the teeth three-fifths as long as the tube; raceme dense; corolla 10 mm. long ..... 30. *A guatemalense*

Pod more or less pubescent.
- Corolla 9–15 mm. long.
  - Corolla white.
    - Stems creeping; stipe shorter than the calyx-tube.
      - Leaflets 25–31, 1–2 cm. long; peduncles 1–4 cm. long; pod 1.5 cm. long or more, rather gradually acute ..... 31. *A. reptans*
      - Leaflets 15–21, less than 1 cm. long; body of the fruit 12 mm. long, abruptly contracted at each end ..... 32. *A Harshbergeri*
    - Stems merely decumbent to erect.
      - Stipe of the pod barely equaling the calyx-tube; body 5–6 mm. broad ..... 33. *A. oaxacanum*

Stipe much exceeding the calyx-tube; body 3–4 mm. wide.
Calyx-teeth subulate, 1.5 mm. long ..... 34. *A. potosinum*
Calyx-teeth deltoid less than 1 mm. long .... 35. *A. altum.*
Corolla purple.
Bracts longer than the calyx-tube; leaflets minutely strigulose beneath ..... 36. *A. bracteatum*
Bracts shorter than the calyx-tube; leaflets sparingly long-pilose beneath ..... 37. *A. Lozani*
Corolla 7–8 mm. long.
Corolla purplish.
Stems low, decumbent; leaflets obovate, often retuse ..... 38. *A. cobrense*
Stems tall, erect; leaflets linear to oblong ..... 39. *A. straturense*
Corolla white or straw-colored.
Stipe equaling or exceeding the calyx-tube.
Pod white-hairy, the stipe much exceeding the calyx-teeth ..... 40. *A. longissimum*
Pod black-hairy, the stipe slightly exceeding the calyx-tube.
Leaves and calyx sparingly short-hairy ..... 41. *A. Rusbyi*
Stem and calyx copiously long-hairy ..... 42. *A. Townsendii*
Stipe shorter than the calyx-tube ..... 43. *A. Rosei*

23. **Atelophragma Painteri** (Rose) Rydb. *Astragalus Painteri* Rose; M. E. Jones, Rev. Astragalus 189. 1923. This species differs from its relatives in the broad and short calyx-lobes. It is very likely the same as *A. strigulosus brevidentatus* Hemsley. (Bot. Cent. Am. **1**: 266. 1880.) I think that Jones made an error when he applied that name to *A. Rusbyi.* The latter has a strigulose pod and very small corolla and is not very closely related to *A. strigulosus.* Besides, *A. Rusbyi* is not found in Central Mexico, as stated by Jones. Jones also referred *Nelson 1427* from Oaxaca to *A. Painteri.* The specimen in the New York Botanical Garden herbarium of this number has subulate calyx-teeth and does not belong here, though I do not know where to refer it as fruit is lacking.

MORELOS: Sierra de Ajusca, *Pringle 6861;* El Parque, *Rose & Painter 7234;* Tres Marias, *Rose & Hay 5314.*

24. **Atelophragma tolucanum** (Rob. & Seat.) Rydb. *Astragalus tolucanus* Rob. & Seat. Proc. Am. Acad. **28**: 164. 1893. This is characterized by the short decumbent stems, shorter peduncles, large bracts, long calyx-lobes and purple conspicuously striate petals. The type came from Nevada de Toluca, State of Mexico, *Pringle 4238.*

25. **Atelophragma jaliscense** Rydb. sp. nov. Perennial, with a cespitose caudex; stems branched, angled, sparingly and finely pubescent with ascending hairs; leaves 5–8 cm. long, ascending; stipules deltoid, about 5 mm. long; leaflets 19–25, oblong or elliptic, 5–10 mm. long, 2–4 mm. wide, obtuse, strigose beneath, glabrate or sparingly pubescent above; peduncles 5–15 cm. long; racemes 3–6 cm. long, bracts subulate, 2–3 mm. long; pedicels very short; calyx more or less black-hairy, the tube 3 mm. long, the teeth subulate, nearly 2 mm. long; corolla white or cream-colored, about 1 cm. long; banner narrowly obovate, moderately arched; wings slightly shorter, the blade linear oblong, falcate, with a large basal auricle; wing-petals still shorter, the blade lunate obtuse; pod glabrous, the stipe 4 mm. long; body lance-linear, tapering at each end, 3–3.5 cm. long, 6–7 mm. broad, a little sulcate on the lower suture, the partial septum 1 mm. wide; seeds 10–11.

Pringle's numbers were named *Astragalus leptocarpus* T. & G., to which it has no relation whatever. Sheldon has suggested *A. Rusbyi* and Jones has named both *A. strigulosus*, to which the species is closely related, differing mainly in the longer, more tapering pod.

JALISCO: Cool slopes, Sierra Tequila, Jalisco, July 5, 1893, *Pringle 4430* (type, in herb. Columbia University).—NUEVO LEÓN: Monterey, *Pringle 2887*.

26. **Atelophragma zacatecanum** Rydb. sp. nov. Perennial; stems rather stout, about 5 dm. high, sparingly short-pubescent with ascending hairs, terete; leaves ascending; stipules deltoid, acuminate, 5–6 mm. long; leaflets 9–15, oblong, 6–15 mm. long, 3–5 mm. wide, strigose beneath, glabrate above, rounded at the apex; peduncles 6–10 cm. long; raceme 5–15 cm. long; bracts subulate, 3 mm. long, calyx long-pilose, the tube 3 mm. long, the teeth fully 3 mm. long, attenuate; corolla cream-colored, 8–10 mm. long, similar to that of the preceeding species, but usually smaller; pod glabrous, the stipe about 4 mm. long, the body oblong, 2–2.5 cm. long, acute at each end, 5 mm. broad, sulcate on the lower suture, the septum narrow, nearly 1 mm. broad; seeds 6–8.

It is related to the preceeding and *A. strigulosum* but differs from both in the long-hairy calyx and longer calyx-teeth, and from the latter in the longer pod. The type was collected in the state of Zacatecas, in 1897, *Rose 2638* (herb. N. Y. Bot. Gard.).

27. **Atelophragma tioides** Rydb. sp. nov. Perennial, cespitose; stems decumbent, much branched, 3–5 dm. high, slender,

terete, strigose; leaves ascending, 5–7 cm. long; stipules deltoid, 3–4 mm. long, leaflets 13–21, obovate, usually retuse at the apex, 5–10 mm. long, 4–7 mm. wide, pilose beneath, glabrate above; peduncles 4–10 cm. long; racemes 3–5 cm. long, rather few-flowered, bracts subulate, 3 mm. long; calyx minutely black-hairy, the tube 3 mm. long, the teeth subulate, 2 mm. long; corolla cream-colored, about 1 cm. long; banner obovate, moderately arched; wings shorter, the blades oblong, slightly falcate; pod glabrous, the stipe very short, shorter than the calyx-tube, the body linear, about 3 cm. long, 5 mm. wide, acute at each end, rather deeply sulcate on the lower suture, the septum narrow; seeds 16–18, dark-brown, 3 mm. long.

It differs from the other species of the group in the narrow pod with very short stipe and the obovate retuse leaflets. Both Schaffner's and Parry & Palmer's specimens were mistaken for *A. leptocarpus*, but the pod is stipitate and its septum only partial and it does not belong to *Hamosa*. On account of its narrow, deeply sulcate pod, it approaches the genus *Tium*.

SAN LUIS POTOSÍ: Valley of San Luis Potosí, in 1876, *Schaffner 822* (type, in Gray Herb.), *617; Parry & Palmer 176*.

28. **Atelophragma strigulosum** (H.B.K.) Rydb. *Astragalus strigulosus* H.B.K. Nov. Gen. & Sp. **6:** 494. 1824. There is some doubt about the identity of this species, as the type was collected in flowers only and the mature fruit was unknown. The ovary, however, is described as being glabrous and stipitate. The plant that fits the description best is the plant of southern Mexico with rather short and broad glabrous pod, abruptly contracted at each end. It is not the plants with strigulose pods of Northern Mexico, Arizona and New Mexico, which Jones included herein and from which the description in his Revision was mainly drawn. Brandegee has mistaken it for the var. *gracilis* Hemsley, which also has a strigulose pod. He distributed *Purpus 2681* under the name mentioned. *Nelson 1940* is cited by Jones under *A. Lozani* but it evidently is closer to *A. strigulosus*, though the leaflets are firmer than usually. *Parry & Palmer 169*, I also refer here, though the stem is stouter and the whole plant is more coarsely hairy. The mature fruit is lacking and the number may represent something else.

SAN LUIS POTOSÍ: (?) *Parry & Palmer 169*.—HIDALGO: Tulancingo, *Rose, Painter & Rose 8835;* Metepec, *Pringle*

10311; 13363; Somariel, *Rose, Painter & Rose 9172.*—PUEBLA: Cerro de Gentile, *Purpus 2681;* Acatzinco, *Arsène 2197;*—OAXACA: Las Naranjas, *Purpus 3209;* between Coixtlahuaca and Tamazulapan, *E. W. Nelson 1940.*—ZACATECAS: *Rose 2638.*—MEXICO: *Bourgeau 400;* Guadelupe, *Rose & Painter 7288;* Toluca, *7913.*

29. **Atelophragma hidalgense** Rydb. sp. nov. Perennial, stem 3–5 dm. high, terete, minutely strigose, branched; leaves 5–7 cm. long; stipules broadly deltoid, 3–4 mm. long, leaflets 19–27, oblong or elliptic, 3–8 mm. long, 1–4 mm. wide, rounded or slightly retuse, minutely strigose beneath, glabrous above; peduncles 3–6 cm. long; racemes short, 6–10-flowered; bracts subulate, 1–2 mm. long; calyx sparingly strigose, the tube 2 mm. long, the teeth linear, scarcely 1 mm. long; corolla 7–8 mm. long, purple-tinged; banner obovate, moderately arched; wings nearly as long, the blade oblong; keel-petals shorter, broadly lunate; pod glabrous, the stipe 1 mm. long, the body elliptic, 12–14 mm. long, about 6 mm. broad, abruptly acute at each end, deeply sulcate on the lower suture, the septum more than 1 mm. wide; seeds about 10.

It is related to *A. strigulosum,* but the flowers are few and smaller, tinged with purple, the calyx less black-hairy and the pod short-stipitate.

HIDALGO: Sierra de la Mesa, July 31 and Aug. 1, 1905, *Rose, Painter & Rose 3132* (type, in herb. N. Y. Bot. Gard.); —MORELOS: *Rose & Hay 5314.*—MEXICO: without locality, *Coulter.*

30. **Atelophragma guatemalense** (Hemsley) Rydb. *Astragalus guatemalensis* Hemsley, Biol. Cent. Am. Bot. **1**: 264. 1880. This is closely related to *A. strigulosum,* differing mainly in the very short stipe, and longer stipules and bracts. Jones gives its distribution as including Oaxaca and Hidalgo. Probably he confused it with the true *Astragalus strigulosus. Ghiesbreght 590,* which was included in Hemsley's *A. strigulosus gracilis* is probably a depauperate form of this. It is not like the type of that variety, which has a strigulose pod.

GUATEMALA: *Gomez* (Donnell Smith's dist.) *1037; Holway 736;* Hacienda de Chaucal, *Nelson 3647.*—CHIAPAS: (?) *Ghiesbreght 590.*

31. **Atelophragma reptans** (Willd.) Rydb. *Astragalus reptans* Willd. Hort. Berol. **2**: 88. 1816. This species is much

larger than the rest and differs in the creeping habit; the flowers, although much larger, resemble those of *A. strigulosum;* the pod has a very short stipe and is black-strigulose. Most herbarium specimens seen consist of a single node and give a poor idea of the whole plant.

MEXICO: (Federal District): *Pringle 6315; Bilimek 107; Vischen,* in 1838.

32. **Atelophragma Harshbergeri** Rydb. sp. nov. Perrennial, stems decumbent or creeping, 2–3 dm. long, slender, glabrous or nearly so; leaves 4–6 cm. long; stipules ovate or rounded, more or less connate, 2–3 mm. long; leaflets 15–21, linear-lanceolate to oblong, acute, 5–10 mm. long, 1–3 mm. wide, strigulose beneath, glabrous above; peduncles 3–5 cm. long, strigulose; racemes about 3 cm. long; bracts subulate, 3 mm. long; calyx black-hairy, the tube 4–5 mm. long, the teeth lance-subulate, 3 mm. long; corolla cream-colored, 12–14 mm. long; banner obovate, slightly retuse, moderately arcuate; wings a little shorter, the blades oblong; fruit minutely black-strigulose, the stipe about 1 mm. long, the body ellipsoid, abruptly contracted at each end, about 15 mm. long, 7 mm. broad.

The type was collected at Salazar, Sierra de las Cruces, August 13, 1896, *J. W. Harshberger 20* (Gray Herbarium). It was originally determined as *Astragalus reptans,* to which it is evidently related, although much smaller. Greenman suggested on the type sheet that it should be compared with *A. strigulosus gracilis* Hemsley, to which it has less affinity.

33. **Atelophragma oaxacanum** (Rose) Rydb. *Astragalus guatemalensis oaxacanus* (Rose) M. E. Jones, Rev. Astrag. 189. 1923. Jones describes this plant as having 'smooth' [the word 'smooth' is invariably used by Jones for glabrous], pod on a stipe longer than the calyx, while in the type cited by him, *Pringle 6264,* the pod is minutely strigulose with rather stiff black hairs and the stipe is barely equaling the calyx-tube. Furthermore Jones stated: 'It is the common form in Mexico from the States of Hidalgo, Mexico, and Oaxaca.' I have seen no other specimens than the type. *Pringle 13263,* determined by Jones as *A. guatemalensis oaxacanus,* belongs to *A. strigulosus,* and *Rose & Painter 7913* named likewise is an undescribed species. Others might have been misdetermined in a similar way.

34. **Atelophragma potosinum** Rydb. sp. nov. *Astragalus strigulosus gracilis* Hemsley, Biol. Cent. Am. 1: 266. 1880.

This species differs from *A. strigulosum* in the smaller flowers and leaflets and the more elongate pod, which is strigose and gradually tapering at each end. The type was collected by Coulter at Zimapan. Hemsley also included a specimen collected in Chiapas, *Ghiesbreght 590*, but this has rose-colored flowers and glabrous pod, and I have referred it doubtfully to *A. guatemalense*.

HIDALGO: Zimapan, *Coulter 631*.—SAN LUIS POTOSÍ: *Schaffner 615–821; Parry & Palmer 175*.

35. **Atelophragma altum** (Woot. & Standl.) Rydb. *Astragalus altus* Woot. & Standl. Contr. U. S. Nat. Herb. **16**: 136. 1913. The type came from Toboggan, Sacramento Mountains, New Mexico. The authors compared it with *A. Rusbyi*, but it differs in the larger flowers and broader pod. It is more closely related to *A. potosinum* (*Astragalus strigulosus gracilis* Hemsl.), differing in the light green foliage, less pubescent calyx and very short calyx-teeth.

NEW MEXICO: Toboggan, *Wooton* in 1899; Clowdcroft, *Slater*, in 1915; Tolerosa Creek, *Wooton*, in 1901, all in Otero County.

36. **Atelophragma bracteatum** Rydb. sp. nov. Perennial, stems 5 dm. high or more, decumbent at the base, sparingly short-pubescent; leaves 5–7 cm. long; stipules lanceolate, acuminate, 5 mm. long; leaflets 13–25, linear-oblong to elliptic, 5–12 mm. long, 2–4 mm. wide, strigose beneath, glabrous above, obtuse to retuse at the apex; peduncles 5–10 cm. long; raceme many-flowered, 3–7 cm. long; bracts lanceolate or lance-linear, 6–8 mm. long, black-hairy and purple-tinged; calyx black-hairy, the tube 4 mm. long, the teeth lance-subulate, 3–5 mm. long; corolla purple, about 1 cm. long; banner obovate, moderately arched; wings shorter, the blade semi-ovate, lunate, with a large auricle; keel-petals broadly lunate, rounded at the apex; pod minutely black-strigose, the stipe about equalling the calyx-tube, the body ellipsoid, 1–1.5 cm. long, 6–8 mm. broad, abruptly contracted at each end; septum less than 1 mm. broad; seeds about 12.

Type collected in October, 1903 on Sierra de Toluca, State of Mexico, *Rose & Painter 7913* (herb. N. Y. Bot. Gard.).

37. **Atelophragma Lozani** (Rose) Rydb. *Astragalus guatemalensis Lozani* (Rose) M. E. Jones, Rev. Astrag. 189. 1923. This differs from *A. strigulosum* and *A. guatemalense* in the

purple flowers, the long pilose pubescence and black-strigulose pod.

HIDALGO: Sierra de Pachuca, *Pringle 6935; Rose & Hay 5587.*

38. **Atelophragma cobrense** (A. Gray) Rydb. *Astragalus cobrensis* A. Gray Pl. Wright. **2:** 43. 1853. This species differs from the rest in the small purple flowers, the strigose, nearly sessile pod and low habit.

NEW MEXICO: Copper Mines, *Bigelow* (Mex. Bound. Surv.) *254;* Silver City, *Greene 1096;* Pinos Atos Mountains, *Greene,* in 1880; Burrow Mountains, *Rusby 91.*

39. **Atelophragma straturense** (M. E. Jones) Rydb. *Astragalus straturensis* M. E. Jones, Contr. W. Bot. **8:** 19. 1898. This resembles *A. Rusbyi* closely in habit, but the corolla is purple and the pod has a much shorter stipe.

UTAH: Silver Reef, *Jones 5175.*

40. **Atelophragma longissimum** (M. E. Jones) Rydb. *Astragalus Rusbyi longissimus* M. E. Jones, Proc. Calif. Acad. II. **5:** 662. 1895. This is closely related to *A. Rusbyi,* to which Jones refers it in his revision, but differs in the long stipe and the white-hairy (not black-hairy) pod.

CHIHUAHUA: Sierra Madre, *Pringle 1219; E. W. Nelson 6283;* Southwestern Chihuahua, *Palmer,* in 1885 (type).

41. **Atelophragma Rusbyi** (Greene) Rydb. *Astragalus Rusbyi* Greene, Bull. Calif. Acad. **1:** 8. 1884. This Jones referred to *A. strigulosus brevidentatus* Hemsley. There is nothing in Hemsley's inadequate description that would indicate a plant from Southwestern United States. Hemsley's type was a cultivated specimen, apparently of Mexican origin. Jones seems to have had a vague idea about *A. Rusbyi,* as he has labeled the duplicate of the type in the Gray Herbarium *A. recurvus* Greene.

NEW MEXICO: Mogollon Mountains; *Metcalfe 428; Wooton,* in 1900.—ARIZONA: Mount Humphry, *Rusby 573,* in 1883; near Flagstaff, *H. C. Hanson 66; MacDougal 233; Jones 3964, 85; Lemmon 3278, Rusby 231;* Mt. Turnbull, *Palmer 107;* Hart's Little Spring, *Toumey 580.* San Francisco Mountains, *Toumey 570 b; Purpus 8010; Knowlton 36; Greene; Leiberg 5684.*

42. **Atelophragma Townsendii** Rydb. sp. nov. Perennial, stem 3–5 dm. high, angled; strigose, somewhat flexuose; leaves 5–8 cm. long; stipules deltoid, 4–5 mm. long; leaflets 15–27, oblong or elliptic to nearly linear, long-pilose on both sides, glabrate in age above, 5–12 mm. long, 1.5–4 mm. wide; peduncles about 1 dm. long, strict; raceme elongate, dense, 5–15 cm. long; bracts subulate, 2–4 mm. long; calyx densely black-hairy, the tube 3 mm. long, the teeth subulate, 1.5 mm. long; corolla cream-colored, about 7 mm. long, banner obovate, strongly arched; wings about as long, the blade broadly lunate; pod black-strigose, the stipe 4–5 mm. long, the body oblong, tapering at each end, about 2 cm. long, 5 mm. wide, deeply sulcate on the lower suture, septum fully 1 mm. broad; seeds about 16.

Jones has determined the type as *Astragalus strigulosus*, to which it is not closely related. It is much nearer *A. Rusbyi*, differing in the longer stipe.

CHIHUAHUA: Sierra Madre, *Townsend & Barber 95;* (type, herb. N. Y. Bot. Gard.); *E. W. Nelson 6174; Jones*, in 1903.

43. **Atelophragma Rosei** (M. E. Jones) Rydb. *Astragalus Rosei* M. E. Jones, Rev. Astragalus 190. 1923. This is closely related to the preceeding three species, differing in the almost sessile pod and long dense inflorescence.

MEXICO (Federal District): Guadelupe, *Rose & Painter 6815;* Amecameca, *O. Kuntze 23647; Holway 5;* Ajusco, *Orcutt 3723.* —PUEBLA: Between Tepeaca and Santa Rosa, *Rose & Hough 4718;* Rancho Pasada, near Puebla, *Arsène & Nicolas 105;* Acatzinco, *Arsène 1596.*

7. SEATONIANA

This section is characterized by the small flowers and fruits. The flowers are less than 5 mm. long, in dense usually short racemes. The latter are less than 1 cm. long, pubescent, sulcate on the lower suture and rounded at each end. Jones included the species in his section *Micranthi*, scattering them among the relations of *A. Hartwegii*, but the pod is one-celled, with only a rudimentary septum, is membraneous and rounded at both ends. Notwithstanding the small size of the flowers and fruit and a different habit the species are most closely related to *A. strigulosum* and its allies.

Stems elongate, 3–4 dm. long; leaflets linear, raceme subcapitate, pods subsessile . . . . . 44. *A. Pueblae*

Stems shorter, 1–3 dm. long, leaflets oblong to obovate; racemes oblong at least in fruit.

Pod subsessile, often black-hairy.....45. *A. Seatoni*
Pod short-stipitate, white-hairy, the stipe nearly as long as the calyx-tube.....46. *A. Purpusi*

44. **Atelophragma Pueblae** (M. E. Jones) Rydb. *Astragalus Pueblae* M. E. Jones, Contr. W. Bot. **14**: 35. 1912. Jones described the pod of this plant as wholly 1-celled and still placed it in 'the parvus group.' The plant and even the pod suggest somewhat the MICROCYSTIS group of *Phaca* and if belonging there would be placed near *P. quinqueflora*. The pod, however, is not turgid, is sulcate on the lower suture and has a trace of a septum. It is essentially that of the next species. It is only known from the type collection from Esperanza, Puebla, *Purpus 5645*.

45. **Atelophragma Seatoni** (M. E. Jones) Rydb. *Astragalus Seatoni* M. E. Jones, Proc. Calif. Acad. II. **5**: 676. 1895. In the original description Jones compared this species with *Astragalus Hartwegii* Benth. The only features common to the two are the small flowers in dense racemes. The general habit is different and so is the pod. The latter is membraneous, somewhat inflated, 1-celled, with a narrow partial septum, all characters indicating *Atelophragma*, but the stipe is obsolete.

PUEBLA: Chalchicomula, *Pringle 8562*.—MEXICO: *Halstedt; Gregg;* Sierra de las Cruces, *Pringle 6445; Bourgeau 337*.—VERA CRUZ: Orizaba, *Seaton 185* (type).—MORELOS: *Pringle 13780*.

46. **Atelophragma Purpusi** (M. E. Jones) Rydb. *Astragalus Purpusi* M. E. Jones, Contr. W. Bot. **14**: 34. 1912. In the original description, Jones placed it in the 'DIDYMOCARPUS-BRAZOENSES,' but in his *Revision*, he transferred it to his MICRANTHI. It resembles so closely the preceding that I have been inclined to include it in the same. The pod (which I have not seen) was described by Jones as stipitate, with a 'stipe nearly as long as the calyx' [not so illustrated]. The young pod is white-hairy and acute, in this respect differing from that of *A. Seatoni*. Only a duplicate of the type *Purpus 4582*, from Sierra de Parras, Coahuila, has been seen.

Mulfordia, a new genus of the Zingiberaceae

H. H. Rusby

(WITH SIX TEXT FIGURES)

The very interesting genus here described was regarded, at the time of its collection, as a species of *Costus* and it was even thought that it might be a variety of *C. Mooreana* Rusby. A slight examination of its structure was sufficient to determine its distinctness from *Costus*, and it was found impossible to assign it to any other known genus.

The plant possesses features of much interest, aside from its generic relationships. Its possession of both outer and inner bractlets is remarkable, and the character of the inner one is altogether unique, so far as my knowledge extends. This sessile bract consists of a body that is closely appressed to the outer or lower surface of the calyx-tube, where it encloses the ovary, and of two wings which surround and enclose the latter. The body, which we may regard as the midrib of the leaf-homologue, is hard and woody, and much thickened. Its inner face closely fits the calyx-tube, being therefore concave, and is very smooth. At its edges, it is two or three times as thick as at the center, the edges being produced dorsally into a stout keel-like or almost alate extension.

The plant, of which but a single specimen was collected, inhabits marshes, growing much like our *Typha*.

Mulfordia, gen. nov.

Calyx coriaceous, nerved, elongated, tubulous, dilated at the base, then contracted, the dilated portion enclosing the ovary, the contracted portion bearing, within, a circle of inflexed scales to which the summit of the ovary is adnate, the remainder of the ovary free. Calyx-limb sub-bilabiate, the lower lip entire, the upper 2-toothed, the teeth coriaceous and erect. Corolla and other parts of the flower not present.

Habit, stem, sheaths and blades as in *Costus*. Flowers densely spicate, bracted and bracteolate. Bracts compressed, concave, partially enclosing the base of the calyx, coriaceous, nerved, bearing at the summit a miniature herbaceous leaf-blade. Bractlets two. Outer bractlet lanceolate and relatively thin. Inner bractlet coriaceous, completely enclosing the calyx-tube, fissured on one side, the other side flattened and somewhat

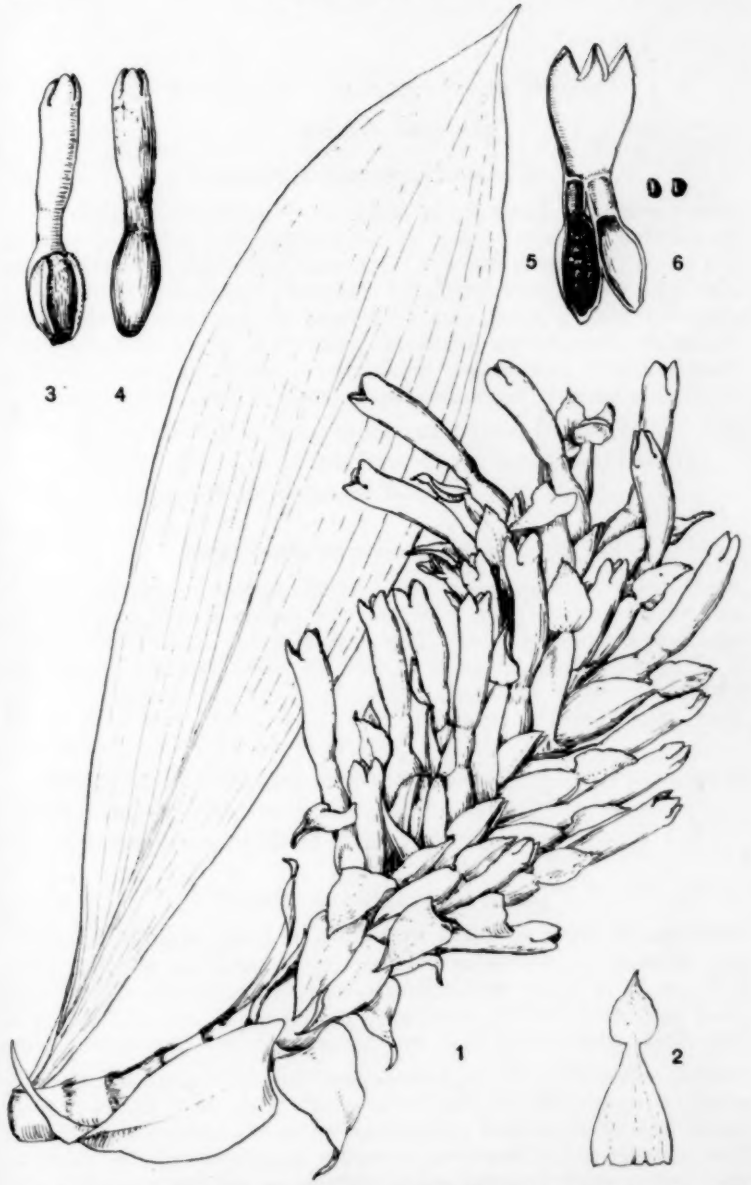
concave, its margins keeled or narrowly winged. Ovary 2-celled, the ovules numerous, horizontal, attached to the margins of the placenta. Seeds numerous, irregularly angled, smooth and shiny. The vestige of a corolla-base, attached to the summit of an immature fruit, is tubular and coriaceous.

The genus is dedicated to the H. K. Mulford Company, through whose generosity the expedition of 1921–22, to the Amazon Valley[1] was made possible.

Mulfordia Boliviana, sp. nov. Stem-sheaths and bracts ciliate, the bracts puberulent. Stems tall and stout, the upper internodes 1 cm. long, 1.5 cm. thick, the sheaths closely appressed, their summits transverse, nearly straight, densely ciliate. Leaf sessile, to 30 by 7 cm., oblanceolate, tapering regularly to the base, short-acuminate and acute, thin, pale-green, especially beneath, the broad midrib paler still and finely nerved. Spike 15 by 8 cm., ovoid, or somewhat obovoid, not very densely flowered, the light-brown bracts thick and coriaceous, about 3.5 cm. long, ovate, puberulent, finely nerved, ciliate, the foliaceous appendages green, 1.5 cm. long and broad, ovate, cordate, acute, puberulent above, sericeous underneath, more or less ferruginous-ciliate. Outer bractlet greenish, rather thin, 2 cm. long, tapering regularly from the base to the acute summit, ciliate. Inner bractlet slightly longer, thick and coriaceous, brown, pubescent, the edges and summit ciliate, enclosing the base of the flower, open on one side, on the other flattened and slightly concave, the edges of the concavity acute or narrowly winged. Stipe of calyx nearly 1 cm. long, stout, the calyx 3 cm. long, nearly 1 cm. wide at the summit, infundibular, with a slight contraction above the dilated basal portion, the summit 3-toothed, one tooth nearly as wide as the other two and resembling a lower lip, the teeth obtuse. Fruit 2 cm. long, 7 cm. wide, oblong, blackish, tuberculate, 2-sulcate, the pericarp very thin. Scales in the throat of the calyx short, thick and tough, irregularly divided, adnate to the upper portion of the ovary. Seeds 3 mm. long, 2 mm. wide, irregularly angularly ovoid, shining, extremely smooth.

Collected by Martin Cardenas at Rurrenabaque, Bolivia, 1000 ft., Nov. 20, 1921 (*No. 1165-A*): type specimen deposited in the herbarium of The New York Botanical Garden.

[1] A general account of the Mulford Expedition was published in Jour. New York Bot. Gard. **23**: 101–112. 1922; and descriptions of new genera and species collected in Mem. New York Bot. Gard. **7**: 205–387. 1927.



Figures 1–6. MULFORDIA BOLIVIANA Rusby. 1. Terminal spike with upper leaf. 2. Bract, with leafy appendage. 3. Young fruit, bearing persistent calyx and inner, 2-keeled bractlet. 4. The same, with bractlet removed. 5. Vertical section of fruit. 6. Seeds. All figures are approximately ⅝ natural size

UNIV OF MICH.

New species of Peperomia from Bolivia[1]

WILLIAM TRELEASE

Peperomia aceramarcana n. sp.

A delicate creeping herb with stout erect branches; stem slender (1 mm.) puberulent; leaves 2–6 at a node, subelliptic, subobtuse at both ends, small (2 × 7–10 mm.), glabrous but subciliolate, glandular-granular beneath, very obscurely subpinnately veined; petiole scarcely 1 mm. long, glabrate; spikes terminal, scarcely 1 × 25 mm., grooved, subzonately flowered; peduncle filiform, about 10 mm. long, puberulent; bracts round-peltate; ovary ovoid, impressed, mucronulate; stigma subapical.

Type locality: Rio Aceramarca at 10,800 ft. (*G. H. H. Tate 713* in 1926,—the type at the New York Botanical Garden.)

Distribution: High Andes of Bolivia.

Peperomia nequejahuirana n. sp.

A stoloniferous-erect herb; stem subsimple, 2 mm. thick, puberulent; leaves commonly about 4 at a node, elliptic-subovate, the lowest suborbicular and the uppermost sometimes suboblong, obtuse, acute at base or cuneate, rather small (1 × 1–2 or 1.5–2 × 2.5 cm.), glabrous, 3-nerved with the midrib branching, dull dark green, paler beneath; petiole 5 mm. long, puberulent; inflorescence unknown.

Type locality: Nequejahuira, at 8,000 ft. (*Tate 642* in 1926, the type at the New York Botanical Garden).

Distribution: Cordillera Real, Bolivia.

Peperomia pitiguayana n. sp.

A moderately small stoloniferous glabrous herb; leaves alternate, elliptic or broadly lanceolate, subacute or acutely protracted, mostly acute at base, moderately small (1 × 2–2.5 or 1.5 × 3–3.5 cm.), drying firm, 5-nerved; petiole 5–10 mm. long; spikes opposite the leaves, as yet 1 × 30–50 mm. and very

[1] The species of *Peperomia* here described pertain to the botanical collections of Mr. G. H. H. Tate, who served as botanical collector on the Ladew Expedition to Bolivia, sent out by the American Museum of Natural History, in 1926. Mr. Tate's collection will probably include 1200 or 1500 species, of which approximately ten per cent will require naming and description. The determination of the species is now being carried on by myself. The *Piperaceae* were referred to Dr. Trelease, who doubtless stands first in knowledge of the Bolivian members of this family.—H. H. RUSBY.

closely flowered; peduncle filiform, 10–15 mm. long; bracts round-peltate.

Type locality: Pitiguaya, Unduavi Valley, at 5,800 ft. (*Tate 722*, the type at the New York Botanical Garden).

Distribution: Cordillera Real, Bolivia.

Peperomia okarana n. sp.

An erect divaricately branching herb; stem 3 mm. thick below, puberulent; leaves commonly about 5 at a node, elliptic-oblanceolate, obtuse or emarginulate, acute at base or subcuneate, very glandular-granular beneath, small (3 × 7, 4 × 12, or 5 × 16 mm.), obscurely papillate above; petiole 1–2 mm. long, glabrate-puberulent; spikes terminal, and verticillate from the upper axils, filiform (scarcely 1 × 20–40 mm.), rather loosely flowered; peduncle 5 mm. long, glabrate; ovary ovoid, mucronulate, impressed; stigma subapical.

Type locality; Okara at 7,500 ft. (*Tate 970* in 1926, the type at the New York Botanical Garden).

Distribution: Cordillera Real, Bolivia.

Peperomia ticunhuayana n. sp.

A spreading soft and subpellucid herb; twigs slender (scant 2 mm.), very evanescently soft-pubescent; leaves alternate, round- to lance-ovate, typically long-acuminate, mostly cordulate, moderate (1.5 × 2–2.5 × 5 cm.), drying very thin, 7-nerved, with the laterals forked, the midrib with about 2 branches, the upper face with a few short thick soft hairs and the nerves beneath somewhat velvety toward the base; petiole about 10 mm. long, hirtellous; spikes opposite the leaves, 1 × 20–50 mm., loosely flowered; peduncle short (scant 5 mm.), subhirtellous; bracts round-peltate; ovary ovoid, mucronate; stigma nearly apical.

Type locality: Ticunhuaya at 5,000 ft. (*Tate 1082* in 1926,—the type at the New York Botanical Garden).

Distribution: Cordillera Real, Bolivia.

THE UNIVERSITY OF ILLINOIS
URBANA, ILLINOIS

INDEX TO AMERICAN BOTANICAL LITERATURE

1926–1928

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